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Fisheries-induced selection as a driver of biodiversity change in exploited populations

Mikko Heino and Ulf Dieckmann

Today, fishing is the dominant source of mortality in most commercially exploited fish stocks. Life-history theory predicts that changes in mortality regime cause selection on life-history traits. In particular, increased mortality can strongly favour earlier maturation. Indeed, commercially exploited fish stocks often show trends towards earlier maturation. However, earlier maturation may also simply reflect phenotypic plasticity – triggered, for example, by improved individual growth when stock abundance is diminished. Until recently, the difficulties involved in disentangling plastic and evolutionary components of life-history changes have hindered understanding the nature of phenotypic maturity changes. Introduction of probabilistic reaction norms for age and size at maturation have helped to combat this problem: by estimating maturation reaction norms, one can control for growth-related phenotypic plasticity and changes in mortality. A suite of methods for estimating these reaction norms is now available. Addressing different types of data, these methods have been applied to about 20 stocks, representing 10 different species of marine and freshwater fish. All but three of these studies suggest that a significant evolutionary component has contributed to the observed trends in age and size at maturation. Remarkably, this component is often detectable at time scales as short as a couple of decades.

Keywords:

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Introduction

Biodiversity is variation of life at all levels of biological organization. Fishing may influence biodiversity of exploited ecosystems at various levels, from species diversity down to genetic diversity within a population of a certain species. One of the main mechanisms of fisheries-induced biodiversity change is selection: some individuals are more likely to survive and reproduce than others, depending on differences in their individual characteristics. Such differences may exist between species (leading to community changes), populations of a certain species (leading to changes in abundance of a species over its range) and individuals within populations, although ultimately selection operates at level of individuals. Here we focus on selection within populations, leading to evolutionary changes when inherited characteristics influence vulnerability to fishing.

There is a ubiquitous trend towards earlier maturation in exploited fish stocks (Trippel 1995). At first glance, this would seem to unambiguously support the hypothesis that fishing

selects for earlier maturation. However, since maturation is a very plastic trait, readily influenced by growth and other factors (Bernardo 1993), it was believed for many years that mere plastic responses to the increased resource availability in stocks fished down to abundances well below pre-industrial levels were sufficient to explain the observed maturation trends. This problem of disentangling plastic and genetic changes in field observations was essentially considered unsolvable. However, as already pointed out by Rijnsdorp (1993), it is possible, through careful statistical analysis, to isolate certain plastic effects in maturation trends. Probabilistic maturation reaction norms offer an elegant solution to such endeavours.

Probabilistic maturation reaction norms

A reaction norm for age and size at maturation describes how variability in growth conditions, reflected by variations in size at age, influences maturation (Stearns and Koella 1986). A probabilistic maturation reaction norm measures the probability with which an immature individual that has reached a certain age and size matures during a given time interval (Heino et al. 2002a). Importantly, this probability is conditional on having reached the considered combination of age and size, i.e., on surviving until, and growing to, this age and size. Through this definition, probabilistic maturation reaction norms (PMRNs) allow considering the maturation process separately from survival and growth effects (see Dieckmann and Heino 2007 for a review). Thus, a main source of plasticity is disentangled. Other sources of plasticity will remain, unless they are included as additional explanatory dimensions in the reaction norm. However, unaccounted sources of plasticity pose a serious problem to detecting evolutionary changes only when they display a trend that parallels presumed evolutionary trend – otherwise, they only add noise around the evolutionary trend.

Methods to estimate probabilistic maturation reaction

The type and scope of available data will dictate which methods are suitable for estimating maturation reaction norms in a particular study. There are three main cases:

- The most informative situation occurs when individuals have been followed from the immature stage to maturity, while at the same time recording their age and size. Unfortunately, this is unlikely with fisheries data. Van Dooren et al. (2005) present an approach to analyse this type of data.
- The next-best situation arises when each individual has been observed only once, but when it is still possible, in each time interval of measurements, to distinguish between three categories of maturation status: immature individuals, individuals that are maturing (or that are newly matured) during the current time interval, and individuals that had matured during earlier time intervals (in other words, juveniles, first-time spawners, and repeat spawners). The *direct estimation method* immediately follows from the definition of probabilistic maturation reaction norms (Heino et al. 2002a): numbers of immature and newly mature individuals sharing a certain combination of age and size can be seen as resulting from independent realizations of the probabilistic maturation process. Unobserved juvenile distributions may be recoverable with reconstruction methods (Heino et al. 2002b).
- Finally, the least informative but still useful case applies when individuals are only classified as either immature or mature, without information to distinguish between newly matured individuals and those that had matured earlier. The basis for the so-called *demographic estimation method* (Barot et al., 2004a, b) is that the processes of recruitment, growth, mortality, and maturation jointly determine a population's demographic composition in terms of maturity status, age, and size. Further, since we are interested in a probability, only relative numbers matter, so that recruitment can be

ignored. With only three demographic processes left in the game, the maturation process can be inferred from demographic composition, provided sufficient information on the other two processes, growth and mortality, is available. Barot et al. (2004a, b) present the estimation procedure starting from standard individual level fisheries data. Marshall and McAdam (2007) present an alternative approach based on aggregated fisheries data (maturity ogives and age-length keys).

Together, these estimation methods comprise a toolbox that allows estimation of PMRNs from many different types of data.

Case studies

The introduction of PMRNs, together with the development of aforementioned toolbox, has opened the way for a large range of case studies where (Table 1). While only certain confounding effects are accounted for (i.e., those related to survival and to growth-related plasticity), the consistency of findings throughout these case studies strongly supports the hypothesis that fisheries-induced evolution towards earlier maturation is commonplace. Remarkably, we see that the pace of fisheries-induced evolution can be very high, leading to detectable changes over just few generations.

Concluding remarks

Available evidence suggests that fishing has already caused widespread evolutionary changes in maturation patterns of wild fish. Almost invariably, these changes are towards earlier maturation at smaller sizes. Similar patterns have been widely observed in fish communities (e.g., Jennings et al. 1998, 1999, Hall 1999. Present fishing practices typically favour fish on the “fast track”, as opposed to unexploited situations where there is also room for fish in the “slow lane”. Whatever is the nature of the change – genetic change, plasticity, or community change – phenotypic diversity of fish life histories is on decline.

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Table 1. Overview of studies where probabilistic maturation reaction norms have been used to facilitate causal interpretation of maturation trends.

Species	Population or stock	Sex (C=combined)	Period with data	Evolutionary trend towards maturation earlier and smaller?	Reference
Atlantic cod *Gadus morhua*	Northeast Arctic	C	1932–2006	Yes	Heino et al. 2002c, in prep.
	Eastern Baltic	F, M	1991–2005	Yes	Vainikka et al., in prep.
	Georges Bank	F, M	1970–1998	Yes	Barot et al. 2004b
	Gulf of Maine	F, M	1970–1998	Yes	
	Northern (2J3KL)	F, M	(1977–)1981–2002	Yes	Olsen et al. 2004
	Southern Grand Bank (3NO)	F, M	1971–2002	Yes	Olsen et al. 2005
	St. Pierre Bank (3Ps)	F, M	1972–2002	Yes	
Haddock *Melanogrammus aeglefinus*	Georges Bank	F, M	1968–2002	Yes	O'Brien et al., in prep.
	North Sea	F	1976–1999	Yes	Wright 2005
Plaice *Pleuronectes platessa*	North Sea	F	1957–2001	Yes	Grift et al. 2003, 2007
American plaice *Hippoglossoides platessoides*	Labrador–NE Newfoundland (2J3K)	F, M	1973–1999	Yes	Barot et al. 2005
	Grand Bank (3LNO)	F, M	1969–2000	Yes	
	St. Pierre Bank (3Ps)	F, M	1972–1999	Yes	
Sole *Solea solea*	Southern North Sea	F	1958–2000	Yes	Mollet et al., in press
Atlantic herring *Clupea harengus*	Norwegian spring-spawning	C	1935–2000	Yes, weak	Engelhard & Heino 2004
	North Sea	F, M	1990–2006	Yes*	Enberg & Heino 2007, in prep.
Small yellow croaker *Pseudosciaena polyactis*	Yellow Sea	C	1985–2001‡ (4 years)	Yes*	Heino, Yin & Dieckmann, in prep.
Chum salmon *Oncorhynchus keta*	Shari River, Hokkaido, Japan	F, M	1992–1997	No§	Morita et al. 2005
Grayling *Thymallus thymallus*	Lake Lesjaskogsvatnet, Norway	C	1903–2000‡ (ca. 15 years)	Yes	Haugen et al. 2008
Small-mouth bass *Micropterus dolomieu*	Opeongo Lake, Ontario, Canada	M	1936–2002‡	No	Dunlop et al. 2005

* Preliminary results ‡ Not a single time series

§ Not a time series study, but empirically established PMRN from data in 1992–1997 was used to interpret changes over 50 years period.